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van der Plas, F., Janzen, T., Ordonez, A., Fokkema, W., Reinders, J., Etienne, R. S., & Olff, H. (2015). A new modeling approach estimates the relative importance of different community assembly processes. *Ecology*, 96(6), 1502-1515. <https://doi.org/10.1890/14-0454.1>

Published in:
Ecology

Document Version:
Publisher's PDF, also known as Version of record

Queen's University Belfast - Research Portal:
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A new modeling approach estimates the relative importance of different community assembly processes

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Abstract. The relative importance of niche-based (e.g., competitive or stress-based) and stochastic (e.g., random dispersal) processes in structuring ecological communities is frequently analyzed by studying trait distributions of co-occurring species. While filtering processes, such as the exclusion of stress-intolerant species from particular habitats, increase the trait similarity between co-occurring species, other processes, such as resource competition, can limit the similarity of co-occurring species. Comparing the observed trait distribution patterns in communities to null expectations from randomized communities (e.g., a draw of the same observed richness from the regional pool) therefore gives a first indication of the dominant process driving community assembly.

However, such comparisons do not inform us about the relative contribution of these different processes in shaping community compositions in case of their joint operation (a likely scenario). Using an Approximate Bayesian Computation approach, we develop a new method that allows inference of the relative importance of dispersal, filtering, and limiting similarity processes for the assembly of observed communities with known species and trait composition. We applied this approach to a tree community data set, collected across 20 plots along strong rainfall and fire gradients in a South African savanna.

Based on comparisons with simulations, we find that our new approach is powerful in identifying which community assembly scenario has the highest probability to generate the observed trait distribution patterns, while traditional null model comparisons perform poorly in detecting signs of limiting similarity. For the studied savanna tree communities, our analysis yields that dispersal processes are most important in shaping the functional trait distribution patterns. Furthermore, our models indicate that filtering processes were relatively most important in areas with high fire frequencies, while limiting similarity processes were relatively most important in areas with low fire frequency and high rainfall. We conclude that our new method is a promising improvement on current approaches to estimate the relative importance of community assembly processes across different species groups, ecosystems, and biomes. Future model modifications (e.g., the inclusion of individual-based processes) could provide further steps in uncovering the underlying assembly processes behind observed community patterns.

Key words: abiotic filters; Approximate Bayesian Computation; community assembly; dispersal; functional traits; Hluhluwe-iMfolozi Park, South Africa; limiting similarity; neutral theory; savanna; stochasticity; trees.

INTRODUCTION

A central goal in community ecology research is to understand the principles that govern the assembly of ecological communities. In order to do so, ecologists have traditionally focused on the importance of niche-based community assembly processes, such as the filtering out of stress-intolerant species under unsuitable abiotic conditions, and the loss of functionally similar species through competitive exclusion (Hutchinson

1959, Weiher and Keddy 1995a, McGill et al. 2006). An alternative view on community assembly has drawn attention to the importance of stochastic processes in community assembly, such as random birth, death, and dispersal events (Caswell 1976, Hubbell 2001). Both views have led to some contrasting theoretical models, in which communities are fully shaped by either deterministic, niche-based processes (e.g., Tilman 1982, Chase and Leibold 2003) or by other processes such as random dispersal (e.g., Hubbell 2001). Current developments in coexistence theory recognize that such models form two extremes of one continuum (Adler et al. 2007), with generally, both stochastic and niche-based processes acting simultaneously to shape community assembly

Manuscript received 5 March 2014; revised 10 October 2014; accepted 18 November 2014. Corresponding Editor: J. Cavender-Bares.

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PLATE 1. In most locations in African savannas, tree densities are not extremely high. Photo credit: F. van der Plas.

(Vellend 2010, Rosindell et al. 2011, Weiher et al. 2011). However, the relative contribution of these processes for different species groups, in different habitats and biomes, and across different spatial scales remains an open question.

A commonly used approach to discriminate between alternative community assembly processes is the analysis of trait diversity patterns of co-occurring species (e.g., Weiher and Keddy 1995b, Cornwell and Ackerly 2009, van der Plas et al. 2012). If niche-based processes are not driving community assembly and dispersal is not limited within a certain region (hereafter called dispersal assembly, *sensu* Kembel [2009]), one would expect a local community to be a random sample from the regional species pool, with a trait distribution that is a random sample from the regional trait distribution. Alternatively, if niche-based processes (such as limiting similarity or filtering) are important in community assembly, one could expect that the diversity of functional traits of co-occurring species deviates from such a random subset. For example, the exclusion of stress- or herbivory/predation-intolerant species or of competitively subordinate species (hereafter collectively called filtering processes) can reduce trait diversity of co-occurring species (Weiher and Keddy 1995a, Cornwell and Ackerly 2009, Mayfield and Levine 2010, Hille-

RisLambers et al. 2012). Instead, competitive exclusion among species with overlapping niches, and exclusion of species with shared (specialist) predators (competition or apparent competition, hereafter collectively called limiting similarity processes) can increase trait or functional diversity (Hutchinson 1959, MacArthur and Levins 1967, Abrams 1983, Violle et al. 2011).

Previous studies have tried to determine whether observed trait variability deviates from dispersal assembly expectations. Although these comparisons can provide a first indication on the dominant process driving community assembly, they are not able to discriminate if patterns not deviating from null expectation are the result of either a lack of niche-based processes, or reflect the net outcome of opposing filtering and limiting similarity processes. Furthermore, the relative contribution of these processes remains uncertain when evaluated using null models, as these are designed to only discriminate between expected, convergent, or even trait distribution patterns. Despite recent improvements in the use of null models (e.g., Helmus et al. 2007, Cornwell and Ackerly 2009, Parmentier et al. 2014), where more information from observed data is used than in traditional ones, the understanding that one can gain from them is still limited. This currently restricts necessary steps toward analyzing and general-

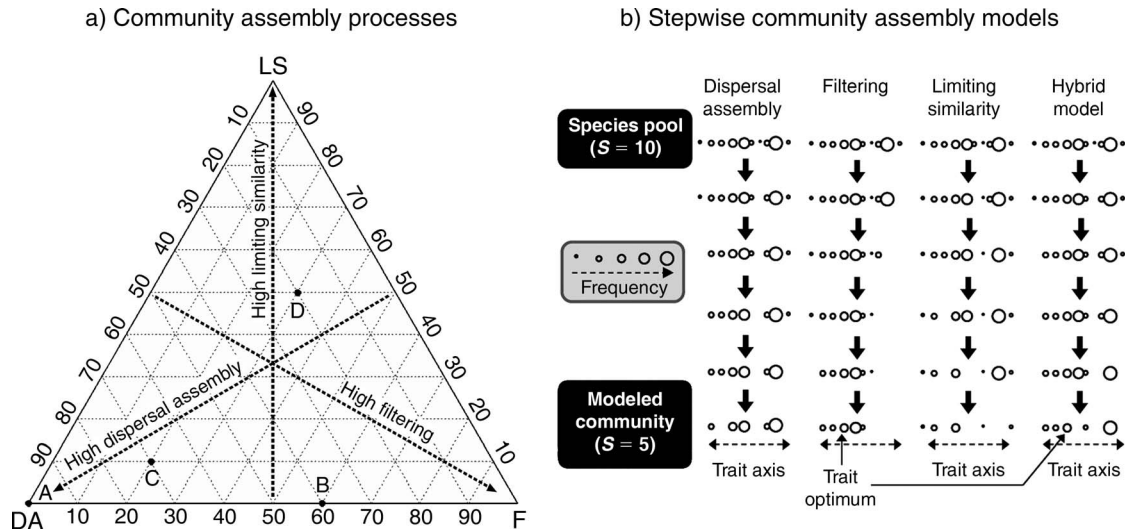


FIG. 1. A graphical illustration of community assembly and stepwise community assembly (STEPSCAM) models. (a) A ternary plot illustrating how community assembly can be seen as the sum of dispersal assembly (DA), filtering (F), and limiting similarity (LS) processes. The distance from each corner represents an axis measuring to what extent (%) community assembly is driven by DA, F, or LS. For any given point in the triangle, corresponding values on each of three axes add up to 100. Letters indicate different example scenarios of community assembly: a community that is (A) 100% assembled by DA; (B) 40% regulated by DA and 60% by F; (C) 70% regulated by DA, 20% by F, and 10% by LS, and (D) 20% regulated by DA, 30% by F, and 50% by LS. (b) An illustration of four different STEPSCAMs. These four models differ in their parameter settings, with from left to the right, a model containing DA steps only, F steps only, LS steps only, and a model consisting of two (i.e., 40%) DA steps, one (i.e., 20%) F step, and two (i.e., 40%) LS steps. In this simple example, each model starts with the same species pool, containing $S = 10$ species. Species are represented by circles, with circle size being proportional to frequency in the species pool and horizontal location reflecting trait value. For simplicity, in this example we focus on a one-dimensional trait space. We set the richness (s) in the local community to 5 species, so that each model consists of $S - s = 5$ steps. At each step, a species is removed, either through DA, in which due to a lack of dispersal limitation, species that occur more frequently in the species pool have a lower chance of being removed, F, in which the species farthest from the trait optimum (arrow) is removed, or LS, in which the species most similar to its neighboring species is removed.

izing how different life-history strategies, habitats, and abiotic conditions determine the relative importance of community assembly processes.

In this study, we develop a new data analysis method that allows (1) the estimation of the relative importance of dispersal, competition, and filtering processes in a community, and (2) analysis of the importance of these different processes along environmental gradients. The basic modeling procedure is based on the stepwise removal of species from an observed regional species pool, until a local community with the observed, actual richness is created. Each step, a species is removed through either a dispersal, filtering, or limiting similarity event, with the relative contribution of these different events differing between alternative models (Fig. 1). So we study the process of stepwise community assembly through the inverse process of stepwise species deletion with stepwise community assembly models (STEPSCAMs). Using Approximate Bayesian Computation (Beaumont et al. 2002, Beaumont 2010, Csillery et al. 2010), we compare the mean trait values and trait distributions of modeled communities with those of real communities. Thereby we identify what the most likely relative importance of dispersal, filtering, or limiting similarity events has been in shaping a particular observed community. Using sensitivity analyses, we

determine whether this new method is able to distinguish different processes of community assembly on the basis of species traits.

We illustrate our STEPSCAM approach by characterizing African savanna tree communities (see Plate 1) along steep rainfall and fire gradients, and comparing their trait distributions with simulated communities to assess which assembly scenarios have most likely operated in nature. African savannas in general (Scholes et al. 2002), and our study site in particular (Whately and Porter 1983), are known for their high habitat heterogeneity. This provides a major challenge for our understanding of local community assembly, since the communities of different habitats are likely shaped by different processes (Cornwell and Ackerly 2009). Other studies emphasized the importance of rainfall (Reed et al. 2009) and fire (Higgins et al. 2007) in structuring savanna plant communities. However, how these environmental gradients regulate changes in communities is largely unknown. Possibly, in more “benign” (high rainfall, low fire frequency) areas, plant communities are mostly shaped by light competition. Alternatively, it might be that in benign areas, all species from the larger regional species pool are also able to cope with the local (a)biotic conditions, so that only dispersal or stochastic

events regulate community assembly, such as suggested for tropical forests (Hubbell 2001).

To test our STEPCAM approach and these ideas, we characterized tree communities and functionally relevant traits in 20 400-m² plots, which were distributed along the rainfall and fire gradients in the study area. We applied our STEPCAM approach and traditional null models to these community data in order to address the following questions: (1) Do trait similarity patterns respond to different community assembly scenarios? (2) If so, to what extent are trait similarity patterns from different community assembly scenarios statistically distinguishable? (3) Which type of community assembly process (dispersal assembly, filtering, or limiting similarity) is most important in shaping savanna tree communities? (4) How do the relative contributions of different community assembly processes change over environmental gradients? (5) Does our STEPCAM approach lead to different conclusions than null models? (6) Do STEPCAMs also create communities with species compositions that are similar to real communities?

METHODS

Calculating functional diversity metrics and trait means

We summarized trait distributions of both observed (see *Tree community, trait data, and environmental gradients*) and simulated communities using four metrics: three multivariate functional diversity metrics, and community trait mean (CTM) values. The three functional diversity metrics we used were developed to be orthogonal and capture different aspects of the functional composition of a community (Villéger et al. 2008): functional richness (FR), functional evenness (FE), and functional divergence (FDiv). FR was measured as the convex hull volume that can be drawn around the multidimensional trait space of all species present in a community (Cornwell et al. 2006). Therefore, FR represents a multidimensional analogue to trait range. For presence-absence data, FE measures the regularity of branch lengths of a minimum spanning tree in multidimensional trait space (Villéger et al. 2008), and thus captures the spacing of species traits, with values bounded between zero (extremely uneven spacing) and one (perfectly even spacing of traits). Lastly, FDiv was measured as the dispersion of measured species in reference to the mean community trait value and thus captures to which extent most trait values deviate from community means. Hence, FDiv is low when most present trait values within FR are near the CTMs (high clustering), and high when most trait values within FR are further away (low clustering) from the CTMs (Villéger et al. 2008). It is important to note that the functional diversity metrics we used are only informative when a minimal number of species are present in communities (Villéger et al. 2008).

Stepwise community assembly models (STEPCAM)

We developed a new statistical modeling framework that simulates community assembly through the stepwise removal of species from a species pool, according to different removal rules reflecting different types of ecological processes. We started with all species from a regional species pool, defined as a collection of S species, with each species having certain traits and a certain frequency (number of occurrences at local sites within the species pool). Then, at each time step, a single species is removed, until the remaining set of species equals the predetermined richness value (s) of a local community under investigation. Therefore, each simulation model contains n steps, where n equals the species richness of the species pool (S) minus the species richness of the local community (s ; Fig. 1). At each step, a species is removed following one of three different mechanisms: (1) dispersal assembly, (2) filtering, or (3) limiting similarity (Fig. 1). For each local community, we generate a series of competing STEPCAMs, differing in the proportion of steps in which each of the three evaluated mechanisms is applied. In each model, first dispersal assembly steps are run, then filtering steps, and finally limiting similarity steps. The implemented order assumes a sequence of community assembly following Cornwell and Ackerly (2009). As a sensitivity analysis, we tested whether this order of community assembly steps highly alters model outcomes, but this was not the case (Appendix: A5).

During a dispersal assembly step, a species is removed from the set of species remaining at that point. The removal chance of each species is inversely proportional to its relative frequency in the species pool (Fig. 1b). Dispersal assembly steps thus represent non-niche-based processes within a region where dispersal is limited, but individuals from different species do not differ in their capacity to disperse, as emphasized in neutral (-like) biodiversity theories (e.g., Caswell 1976, Hubbell 2001).

During a filtering step, the species with trait values with the largest Euclidean trait distance from the trait optima (defined as the CTM values of observed communities, thereby assuming that observed assemblages represent the best suite of traits under particular environmental conditions; Keddy 1992) of the community under investigation is removed from the remaining species set (Fig. 1b). These filtering steps, which are based on Kraft et al. (2007), can be seen as niche-based processes where species without the right traits are unable to occur in a particular abiotic (Weiher and Keddy 1995a, Cornwell et al. 2006) or biotic (Mayfield and Levine 2010, HilleRisLambers et al. 2012) environment.

Lastly, during a limiting similarity step, we identify from the remaining species set the species pair closest to each other in the multidimensional trait space. From this pair, we remove the species closest to a third species (Fig. 1b). This step, adapted from Kraft et al. (2007), reflects the exclusion of species with shared resources (Hutchinson 1959, MacArthur and Levins 1967,

Abrams 1983, Violle et al. 2011), predators, or pathogens (Abrams 1983).

Responses of functional diversity metrics to community assembly scenarios

To explore whether and how FR, FE, and FDiv values respond to different relative contributions of dispersal assembly, filtering, and limiting similarity steps, we applied several STEPCAMs over a range of parameter settings to one of the plots (Plot 17) evaluated in this study, which was considered most representative (see *Tree community, trait data, and environmental gradients* for our rationale). Although it would have been possible to explore responses of FD patterns to community assembly models for more plots than Plot 17 only, we chose to focus on one (representative) plot only due to the long computational time (several weeks per plot) it would have taken to focus on other plots as well. The regional species pool was defined as all S (105) species found across the 20 observed plots (see *Tree community, trait data, and environmental gradients*), with the number of plots in which each species was found as the species frequencies. Plot 17 had $s = 15$ species, so each STEPCAM consisted of $S - s = 90$ steps. In each different STEPCAM, the relative contributions of dispersal assembly, filtering, and limiting similarity steps add up to 1. We explored this parameter space with 0.05 intervals, so we ran models with parameter settings of 1:0:0, 0.95:0.05:0, 0.95:0:0.05, 0.9:0.1:0, 0.9:0.05:0.05, etc., in which the first number stands for the relative contribution of dispersal assembly steps, the second number for the relative contribution of filtering steps, and the last number for the relative contribution of limiting similarity steps. Consequently, we ran 231 different generator models (also used for sensitivity analyses) with 1000 replicates for each.

We summarized FR, FE, and FDiv patterns for each model as the average across all 1000 replicates. For more details on this methodology, we refer to Appendix: A4. STEPCAMs were run with the STEPCAM R package (Janzen and van der Plas 2014).

STEPCAM fitting: general procedure

To compare the fit of summary statistics of competing STEPCAMs with the summary statistics from observed data (i.e., from communities observed in the field; see *STEPCAM fitting: observed communities*) or from communities created by a generator model (see *STEPCAM fitting: sensitivity analysis*), we used Approximate Bayesian Computation (ABC) within a Sequential Monte Carlo (SMC) framework (Toni et al. 2009, Hartig et al. 2011). ABC compares one or more summary statistics between observed data and candidate models. Previous to model selection, the four summary statistics (FR, FE, FDiv, and CTM values, calculated for 20 communities) were standardized to a mean of 0 and a standard deviation (SD) of 1, by subtracting mean values from observed values and then dividing by the

SD. This way, each different summary statistic had the same impact on the fitting procedure. The fit of candidate STEPCAMs was calculated as: $\text{Fit}_{\text{total}} = \text{Fit}_{\text{FR}} + \text{Fit}_{\text{FE}} + \text{Fit}_{\text{FDiv}} + \text{Fit}_{\text{CTM}}$, in which Fit_{FR} , Fit_{FE} , Fit_{FDiv} , and Fit_{CTM} are the absolute (multidimensional) difference between, respectively, observed FR, FE, FDiv, and CTM values and those functional diversity and CTM values generated by the candidate STEPCAM. High $\text{Fit}_{\text{total}}$ values thus indicate poor fit, while low values indicate good fit. Using the fit of the models, importance resampling was performed largely following the algorithm described in Toni et al. (2009). For more detailed information on the algorithm we used, refer to Appendix: Figs A6 and A7.

STEPCAM fitting: sensitivity analysis

As a sensitivity analysis, we investigated whether generator STEPCAMs with the different community assembly scenarios generate communities with statistically distinguishable trait distributions, in addition to quantitatively different trait distributions as were described in *Responses of functional diversity metrics to community assembly scenarios*. The summary statistics that resulted from the generator models were fitted with an ABC-SMC approach (described in *STEPCAM fitting: general procedure*) to yield the best-fitting (STEPCAM) models. Each generator STEPCAM and the refitting procedure were run 10 times with different random seeds, as ABC-SMC is inherently stochastic. Due to the long computational time (several weeks), we did not run more than 10 random seeds, although the variation among the outcomes using different seeds was low enough to justify this (Appendix: Fig. A7A). We then investigated to what extent the average (across 10 random seeds) parameter values (proportion of dispersal assembly, filtering, and limiting similarity steps) of the generator models and the best-fitting models differed, in order to assess to what extent the ABC-SMC procedure can successfully distinguish STEPCAMs with different community assembly scenarios.

STEPCAM fitting: observed communities

After assessing whether STEPCAMs with different community scenarios generate communities with different trait distributions, we used the same ABC-SMC approach to fit the functional diversity and CTM values of the communities (plots) observed in the field (see *Tree community, trait data, and environmental gradients*). Thereby, we investigated which community assembly scenario most likely operated in the field. For each plot, we ran the algorithm 10 times with different random seeds (all with uninformative priors). For each plot, inferred parameters are the mean of 10 replicate ABC-SMC procedures. Standard deviations of posterior distributions can be seen in Appendix: Fig. A7A–C. STEPCAM fitting was done with the STEPCAM R package (Janzen and van der Plas 2014).

TABLE 1. Descriptions of the 20 study plots in Hluhluwe-iMfolozi Park, South Africa.

Plot	Latitude (°S)	Longitude (°E)	Rainfall	Fire freq.	SLA	LA	WD	C	N	P	S	K
1	28.08	32.04	837.08	11	139	19.3	0.80	47.2	2.31	38.6	67	376
2	28.12	32.03	746.20	15	139	5.6	0.82	45.5	2.21	40.8	86	377
3	28.13	32.04	725.45	18	123	8.3	0.85	47.2	2.52	51.3	101	348
4	28.15	32.01	635.36	8	112	5.8	0.87	45.6	2.02	40.6	117	330
5	28.18	31.98	676.91	19	107	2.3	0.92	47.8	2.60	49.1	126	307
6	28.28	31.97	640.16	18	112	7.6	0.82	45.9	3.03	50.2	101	538
7	28.28	31.88	578.38	10	121	2.5	0.90	46.0	2.48	50.1	138	330
8	28.23	31.83	556.55	10	127	5.3	0.91	45.5	2.47	41.3	88	449
9	28.25	31.81	539.26	11	116	4.3	0.86	46.7	2.41	47.1	104	391
10	28.20	32.00	692.24	24	105	2.9	0.85	47.4	2.55	49.4	93	337
11	28.19	31.90	696.05	23	108	3.8	0.90	46.4	2.39	45.3	101	397
12	28.10	32.12	726.51	8	153	12.5	0.78	45.6	2.48	57.2	96	446
13	28.07	32.12	744.59	22	127	5.6	0.89	46.8	2.66	53.8	109	371
14	28.05	32.05	816.37	10	140	18.4	0.85	46.7	2.18	33.4	62	381
15	28.18	31.98	672.91	10	103	4.1	0.90	47.1	2.39	45.6	130	311
16	28.23	32.02	705.65	21	123	0.1	0.92	47.8	2.85	55.2	128	318
17	28.19	32.00	669.09	12	106	12.0	0.85	47.5	2.33	43.0	70	337
18	28.13	32.04	711.34	15	121	5.8	0.81	47.3	2.20	50.5	84	369
19	28.29	31.75	555.01	16	87	0.9	0.91	47.4	2.70	42.0	150	380
20	28.28	31.74	548.09	15	137	4.4	0.88	44.4	2.71	38.3	69	711
Mean	28.18	31.97	673.66	15	120	6.6	0.86	46.6	2.48	46.1	101	390

Notes: Traits are given as the unstandardized community-abundance-weighted mean values in each plot. Fire frequency is calculated as number of fires between 1956 and 2004, and rainfall is shown in mm/yr. Other traits include specific leaf area (SLA; cm²/g), leaf area (LA; cm²), wood density (WD; kg/L), leaf C and N (dry mass percentage), and leaf P, S, and K (mmol/kg). Values of Plot 17 were used in sensitivity analyses.

Tree community, trait data, and environmental gradients

We compared how well traditional null models and our STEPCAM approach can link trait distributions with the three alternative community assembly processes outlined by applying both methods to savanna tree communities. For this, one needs to collect the following data: (1) a species–plot presence matrix; in our specific case, community composition data of trees along main environmental gradients, and (2) a species trait matrix; in our case, measurements of several functional traits for each observed tree species.

The study site was situated in Hluhluwe-iMfolozi Park (HiP; 28°00'–28°26' S, 31°41'–32°09' E), South Africa. The ~90 000-ha reserve is characterized by high habitat heterogeneity (Whateley and Porter 1983), with upland forests, savanna grassland and thickets, woodlands, and riverine forests. At larger scales, this vegetation heterogeneity arises from environmental gradients in rainfall and fire regimes (Balfour and Howison 2002, van der Plas et al. 2012). From November till December 2009, tree species composition (trees over 0.5 m high) and trait information were characterized in a total of 20 plots (measuring 20 × 20 m) along these gradients. The eight measured eco-morphological traits were specific leaf area, leaf area, wood density, and leaf carbon, nitrogen, phosphorus, sulfur, and potassium content. These traits were selected due to their relation with growth–longevity trade-offs, drought tolerance, nutritional status, and attractiveness to herbivores (e.g., Brown and Lawton 1991, Marschner 1995, Weiher et al. 1999, Hacke et al. 2001, Westoby et al. 2002). A detailed description of the study site and the data collection protocol, as well as

detailed plot information, is presented in Tables 1 and 2 and Appendix: Tables A1–3.

For each species/trait combination, we calculated the species average trait values (hereafter species trait values). Missing species trait values (25.9% of values; values were mostly missing for rare species) were completed using multiple imputation with chained

TABLE 2. Community descriptions of the 20 plots in the study area.

Plot	Species richness	Abundance	FR	FE	FDiv
1	27	319	56.69	0.61	0.86
2	16	417	6.02	0.37	0.73
3	23	1640	12.08	0.44	0.85
4	24	906	22.76	0.66	0.64
5	10	375	0.92	0.47	0.57
6	17	1144	14.42	0.61	0.92
7	14	511	2.54	0.65	0.58
8	23	568	6.07	0.47	0.65
9	13	344	4.82	0.74	0.82
10	9	266	2.68	0.28	0.65
11	5	109	0.03	0.41	0.89
12	12	342	18.09	0.58	0.85
13	15	653	21.47	0.54	0.66
14	18	656	16.38	0.55	0.94
15	13	261	6.94	0.53	0.73
16	5	322	0.06	0.35	0.74
17	15	288	9.58	0.58	0.71
18	13	167	5.99	0.64	0.62
19	8	271	0.57	0.67	0.50
20	8	454	3.16	0.39	0.98
Mean	14.4	501	11.01	0.53	0.74

Notes: Traits are given as the unstandardized community-abundance-weighted mean values in each plot. Abundance is calculated as number of tree stems >0.5 m height per plot. Functional diversity values, functional richness (FR), evenness (FE), and divergence (FDiv), are based on standardized trait values.

equations (MICE), using the mice function from the mice package (Van Buuren and Groothuis-Oudshoorn 2011) in R v. 2.13.1 (R Development Core Team 2011). The MICE imputation process involves specifying a multivariate distribution for the missing data, and drawing imputation from their conditional distributions by Gibbs sampler techniques (a valid approach if a multivariate distribution is a reasonable description of the data as in the case of trait values). Prior to other analyses, all species trait values were globally standardized (mean = 0, SD = 1). As such, we avoided those traits whose higher mean or variance had a higher impact on model outcomes. Species trait values were used to calculate functional diversity metrics (using the dbFD function from the FD package; Laliberté and Shipley 2011) and CTM values for each plot (see *Calculating functional diversity metrics and trait means*), using R v. 2.13.1 (R Development Core Team 2011). Data on environmental gradients (long term annual rainfall in mm/yr and number of fires between 1956 and 2004) were acquired from the HiP management authorities and are described in Appendix: Table A1. As Plot 17 was most representative with its geographical location, intermediate annual rainfall, fire frequency, species richness, abundance, and functional diversity values (Tables 1 and 2), we studied this plot in more detail to see how functional diversity metrics respond to community assembly processes and whether the ABC-SMC approach could distinguish between the outcomes of different STEPCAMs (see *Responses of functional diversity metrics to community assembly scenarios and STEPCAM fitting: sensitivity analysis*).

Relationships between tree community assembly and environmental gradients

Relative contributions of dispersal assembly, filtering, and limiting similarity steps of the STEPCAMs best fitting the observed 20 communities (identified in *STEPCAM fitting: observed communities*) were not independent of each other, and were therefore analyzed simultaneously, using multivariate analysis of variance (MANOVA). Fire, rainfall, and their interaction effect were used as predictor variables. Only relative contributions of filtering and limiting similarity steps were included in the MANOVA, because the relative contribution of dispersal assembly and filtering steps appeared to be tightly correlated among sites ($r = -0.901$; a logical consequence when these two processes dominate but are also constrained to a sum that cannot exceed 1). The relative contribution of dispersal assembly steps was therefore separately analyzed using a general linear model. With general linear models and a model selection procedure, we additionally explored how CTM values changed over environmental gradients, to help interpreting STEPCAM results. Initially, full models were created, containing annual rainfall, fire frequency, species richness, and log abundance of individual trees as predictor variables. We then ran a maximum likelihood model-selection procedure in order to identify the (nested)

model structure with the lowest Akaike information criterion (AIC) value. These analyses were performed using R v. 2.13.1 (R Development Core Team 2011). Outcomes of this are presented in Appendix: A8.

Comparing species compositions of observed communities with simulated communities

With our STEPCAM approach, we attempted to gain insight in community assembly by fitting functional compositions of observed communities. If best-fitting STEPCAMs (identified in *STEPCAM fitting: observed communities*) truly reflect community assembly in nature, one might expect that species compositions of modeled communities should also be similar to observed ones (but see Fukami et al. 2005). We investigated this question by quantifying community compositions of both observed communities and communities created by best-fitting STEPCAMs into nonmetric multidimensional scaling (NMDS) axes. NMDS analyses were based on the Bray-Curtis dissimilarity index (Bray and Curtis 1957) with three axes. We performed 100 iterations and achieved a minimal stress level of 0.190 ($r^2 = 0.780$). We then explored whether NMDS axes of observed communities correlated with NMDS axes of associated best-fitting communities. Using the envfit function in the vegan package (Oksanen et al. 2013), we assessed to which extent environmental variables relate to ordination axes based on Pearson correlation coefficients of ordination points with the environmental variables.

Null models

We used traditional, permutation-based null models (Gotelli and Entsminger 2001) to assess whether functional diversity values observed in each plot were higher or lower than expected by chance and to determine how conclusions based on null model outcomes differ from conclusions based on STEPCAM results. For each plot, we created 1000 randomized communities based on a randomized sampling of the species pool found in our study (i.e., all species observed), where the chance of a species being selected was equal to its relative frequency in the region (i.e., the number of plots in which it was observed). As a sensitivity analysis, we also performed a pure null model where the chance of drawing a species is frequency independent. Each randomized draw was constrained to have the same richness as the observed community.

Deviation from the null expectation was determined using the number of times that observed FR, FE, and FDiv values were higher or lower than the functional diversity values from randomly generated null communities (i.e., two-sided test, $\alpha = 0.05$; Gotelli and Graves 1996). If observed functional diversity is greater than the null prediction in 975 or more cases (i.e., a ratio of 0.975), limiting similarity processes are assumed to have formed the community. Alternatively, if observed is greater than null in 25 or fewer cases (i.e., a ratio of

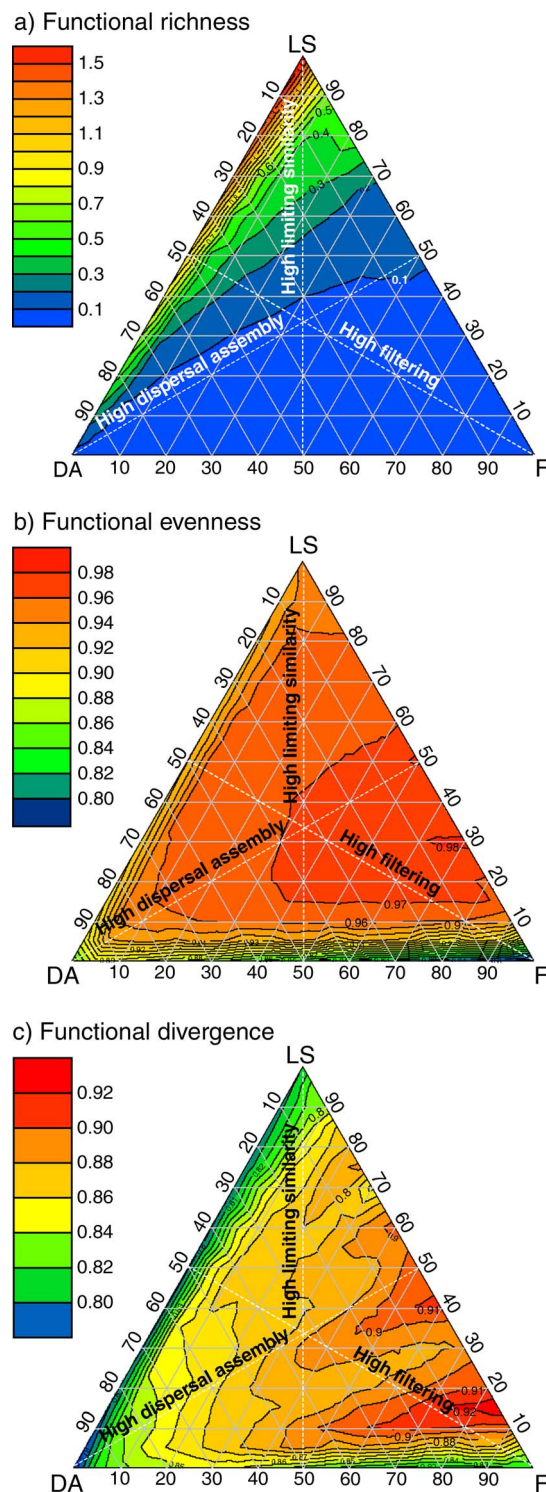


FIG. 2. Ternary plots with the responses of functional (a) richness, (b) evenness, and (c) divergence to changes in the relative contribution of DA, F, and LS steps in STEPCAMs. Functional diversity values are estimates based on 231 STEPCAMs applied to Plot 17 at our study site (Hluhluwe-iMfolozi Park, South Africa). Functional diversity values for other positions in parameter space were estimated using bilinear interpolation using the `interp` function of the `akima` package

(0.025), then filtering is assumed to be the central process in community assembly.

RESULTS

STEPCAMs: responses of functional diversity metrics to community assembly scenarios

To investigate how multivariate functional diversity metrics likely respond to different community assembly scenarios, we investigated functional diversity patterns of communities generated by different STEPCAMs. FR was lowest in species assemblages formed by STEPCAMs where filtering steps were relatively important and highest in species assemblages that were mostly formed by STEPCAMs with a high relative importance of limiting similarity processes (Fig. 2). FE and FDiv were low in communities formed by STEPCAMs only including filtering or dispersal assembly steps, and higher in communities mostly formed by limiting similarity steps (Fig. 2). However, STEPCAM simulations show that FE and FDiv values were even higher in communities that were partially formed by filtering and partially by limiting similarity (Fig. 2).

STEPCAMs: sensitivity analyses

Although functional diversity values changed with parameter settings, another question is whether functional diversity values created with different community assembly scenarios are also statistically distinguishable. Fitting of the trait patterns resulting from generator STEPCAMs showed that the trait distribution patterns from STEPCAMs with different parameters are indeed distinguishable with the ABC-SMC fitting procedure. On average, parameter settings of the best-fitting models hardly differed from their associated generator models (Appendix: Fig. A7D): average parameter deviations were 3.8% for dispersal assembly, 2.2% for filtering, and 2.0% for limiting similarity. This was much lower than the 27.7% deviation that one would expect for each parameter value if the ABC-SMC approach was completely uninformative (Appendix: Fig. A7E). Furthermore, parameter settings of the best-fitting models highly correlated with those of generator models (all $r^2 > 0.95$; Appendix: Fig. A7F). These checks thus suggest that observed trait distributions can be accurately linked with community assembly scenarios. Furthermore, changing the order of different community assembly processes (e.g., a random order of dispersal assembly, filtering, and limiting similarity processes) did not highly alter functional diversity patterns resulting from modeled communities (all r^2 values of functional diversity metrics generated by STEPCAMs with different order of community processes > 0.89 ; Appendix: Fig. A5), suggesting that changing the order of different commu-

(Akima et al. 2009) in R (R Development Core Team 2011). All abbreviations are as in Fig. 1. Axis numbers are percentages.

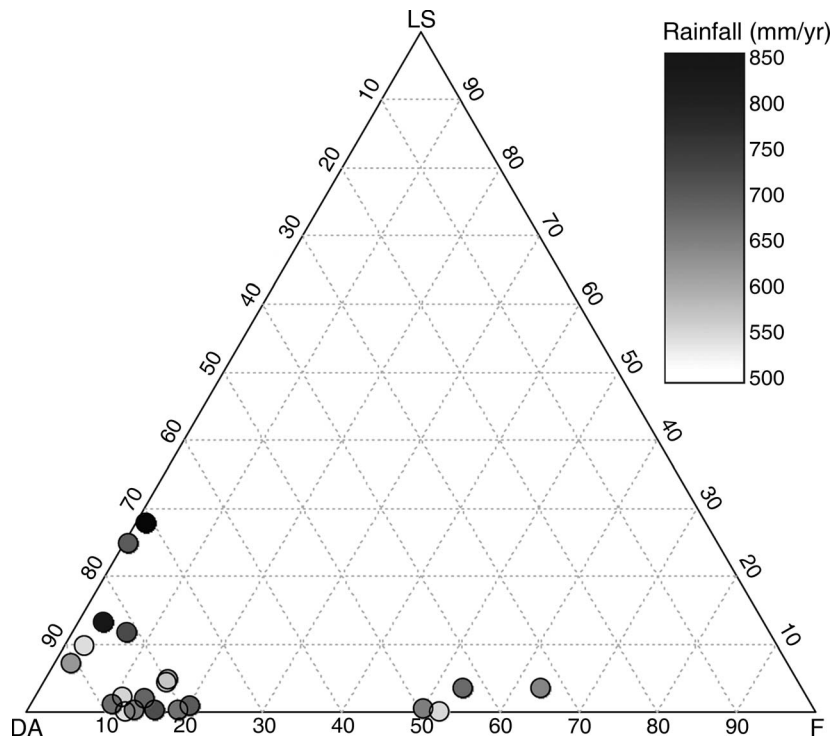


FIG. 3. Ternary plot with the dots representing the best-fitting STEPCAM for each of the 20 plots in Hluhluwe-iMfolozi Park. All abbreviations are as in Fig. 1. Axis numbers are percentages.

nity assembly processes would not highly affect the outcomes of our fitting procedure (Appendix: Fig. A5A).

STEPCAM application: what structures savanna tree communities?

When STEPCAMs were fitted to trait distribution values of the 20 observed savanna tree communities using the ABC-SMC approach, best-fitting models had a high relative contribution of dispersal assembly steps (75.8% average across plots), a lower relative contribution of filtering steps (18.8% average across plots), and even fewer limiting similarity steps (5.4% average across plots; see Fig. 3 for parameter values for each plot). Posterior distributions of accepted model parameters generally had narrow ranges and did not differ highly between replicate models (Appendix: Fig. A7), indicating that the ABC-SMC approach is adequate in detecting best-fitting STEPCAMs. A MANOVA showed that limiting similarity steps had the relatively highest contribution in best-fitting models in plots with high rainfall, especially when fire frequency was low (rain effect, $T = 3.372$; $P = 0.004$; fire effect, $T = 1.969$; $P = 0.066$; rainfall \times fire frequency interaction, $T = -2.191$; $P = 0.044$; model $r^2 = 0.401$; Fig. 4), while filtering was most important in plots with high fire frequency and low rainfall (Fig. 4; rainfall effect, $T = 2.088$; $P = 0.053$; fire effect, $T = 2.705$; $P = 0.016$; rainfall \times fire frequency interaction effect, $T = -0.503$; $P = 0.024$; model $r^2 = 0.645$; Fig. 4). So, we found statistical evidence that

limiting similarity became more important toward high rainfall (co-occurrence of less similar species), while a high fire frequency promotes co-occurrence of similar species. An additional multiple regression model shows that the relative contribution of dispersal assembly in best-fitting models decreases with rainfall and fire ($T = -3.008$, $P = 0.008$; $T = -3.136$, $P = 0.006$ respectively), while an interaction effect between rainfall and fire also exists ($T = 3.019$, $P = 0.008$; $r^2 = 0.332$).

Comparison of observed and modeled community compositions

NMDS analyses demonstrate that even while our ABC-SMC approach only fits functional data of simulated communities to observed ones, species compositions of simulated communities are also fairly similar to observed ones. Species compositions of simulated and observed communities occupied similar positions in NMDS space (Fig. 5a). Furthermore, ordination values of the first two out of three NMDS axes of observed and associated simulated communities correlated significantly (NMDS1, $r^2 = 0.286$, $P = 0.009$; NMDS2, $r^2 = 0.388$, $P = 0.004$; NMDS3, $r^2 = 0.058$; $P = 0.157$; Fig. 5b–d).

Comparison to null models

In three plots, FR was lower than expected by chance (i.e., lower than in 97.5% of the random draws), while lower FE and FDiv values than expected by chance were

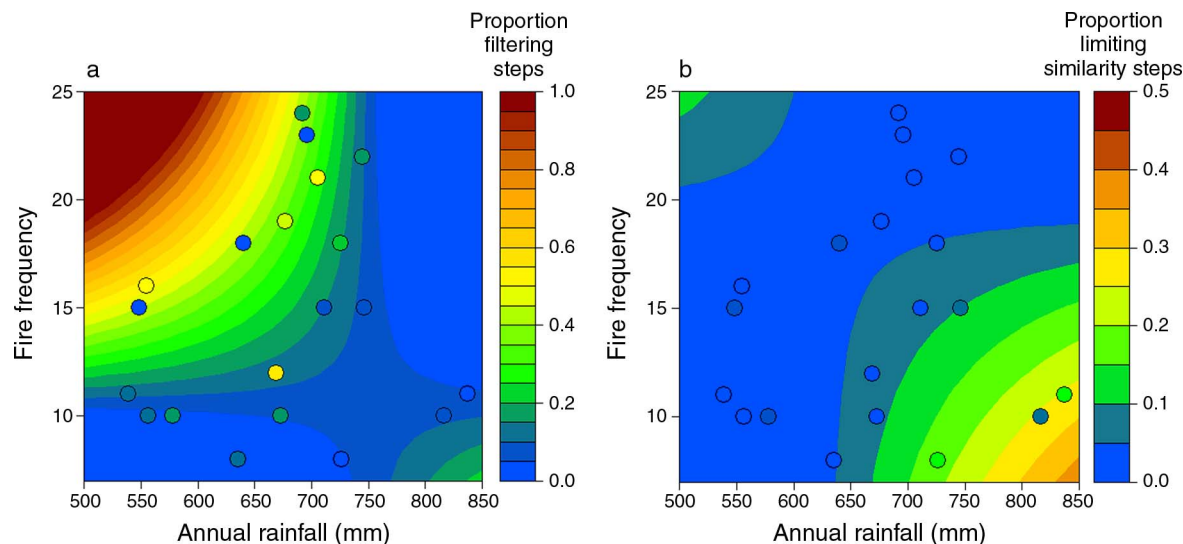


FIG. 4. Contour plot with the contours showing expected (based on MANOVA outcomes) relative contribution of (a) F and (b) LS steps of best-fitting STEPCAMs, as a function of rainfall and fire frequency (number of fires between 1956 and 2004). Best-fitting model parameters, used as input for the MANOVA, are plotted as points. Colors range from blue (focal process is unimportant) to brown (given process explains 100%, or 50% in case of limiting similarity, of community assembly). High similarity between colors of points and their background indicates high model fit, while low similarity indicates low model fit; r^2 values are 0.40 (F) and 0.65 (LS).

found in two plots. When null models were not frequency weighted, FR was lower than expected by chance in six plots, while results for FE and FDiv did not change qualitatively. Functional diversity values significantly higher than expected by chance (suggesting limiting similarity) were never found, so all other plots had functional diversity values not deviating from random. Null model deviations (proportion of permutations were a functional diversity metric that was higher than expected) generally correlated weakly with STEPCAM outcomes: all functional diversity measure deviations correlated negatively with the proportion of filtering steps of best-fitting STEPCAMs ($r = -0.086$, -0.535 , and -0.306 for FR, FE, and FDiv respectively) and positively with the proportion of limiting similarity steps ($r = 0.650$, 0.195 , and 0.165 for FR, FE, and FDiv respectively).

DISCUSSION

To estimate the relative contribution of dispersal assembly, filtering, and limiting similarity processes in community assembly, we used our novel STEPCAMs and the ABC-SMC model selection approach for each of the 20 savanna tree communities investigated. Several authors have suggested that community assembly processes are very difficult to separate when operating simultaneously, because effects of filtering and limiting similarity on trait distribution patterns can cancel each other out (Kraft et al. 2007, Weiher et al. 2011). However, the fitting of trait distribution patterns generated with known parameter settings showed that it is possible to distinguish between different commu-

nity assembly scenarios with varying importance of different processes. This indicates that the use of STEPCAMs as expectation generators, combined with the use of an ABC approach for discrimination between alternative STEPCAMs for the same observed data set, allows us to statistically disentangle the relative importance of different community assembly processes. Additionally, when repeatedly fitting STEPCAMs to the same data, the ABC-SMC consistently selected best-fitting models with approximately the same community assembly scenarios. This demonstrates that our STEPCAMs generate repeatable trait distribution patterns. Moreover, we found that species compositions of simulated communities were fairly similar to observed ones. It is certainly not trivial that species-based community assembly should be possible to predict from functionally based community assembly (Fukami et al. 2005), and it is therefore very promising that simulated communities nevertheless have species compositions similar to observed ones. We suggest that the main reason for this success is the fact that we simultaneously fitted multiple independent summary statistics (FR, FE, FDiv, and CTM values) so that we used more information of observed data sets than traditional analyses do. While different community assembly scenarios might lead to communities with similar FR, FE, FDiv, or CTM values alone (Fig. 2), these are unlikely to shape communities in which all aspects of the trait distribution are the same.

Although other approaches of estimating the relative contribution of different processes in shaping communities have recently been developed (e.g., Laughlin et al.

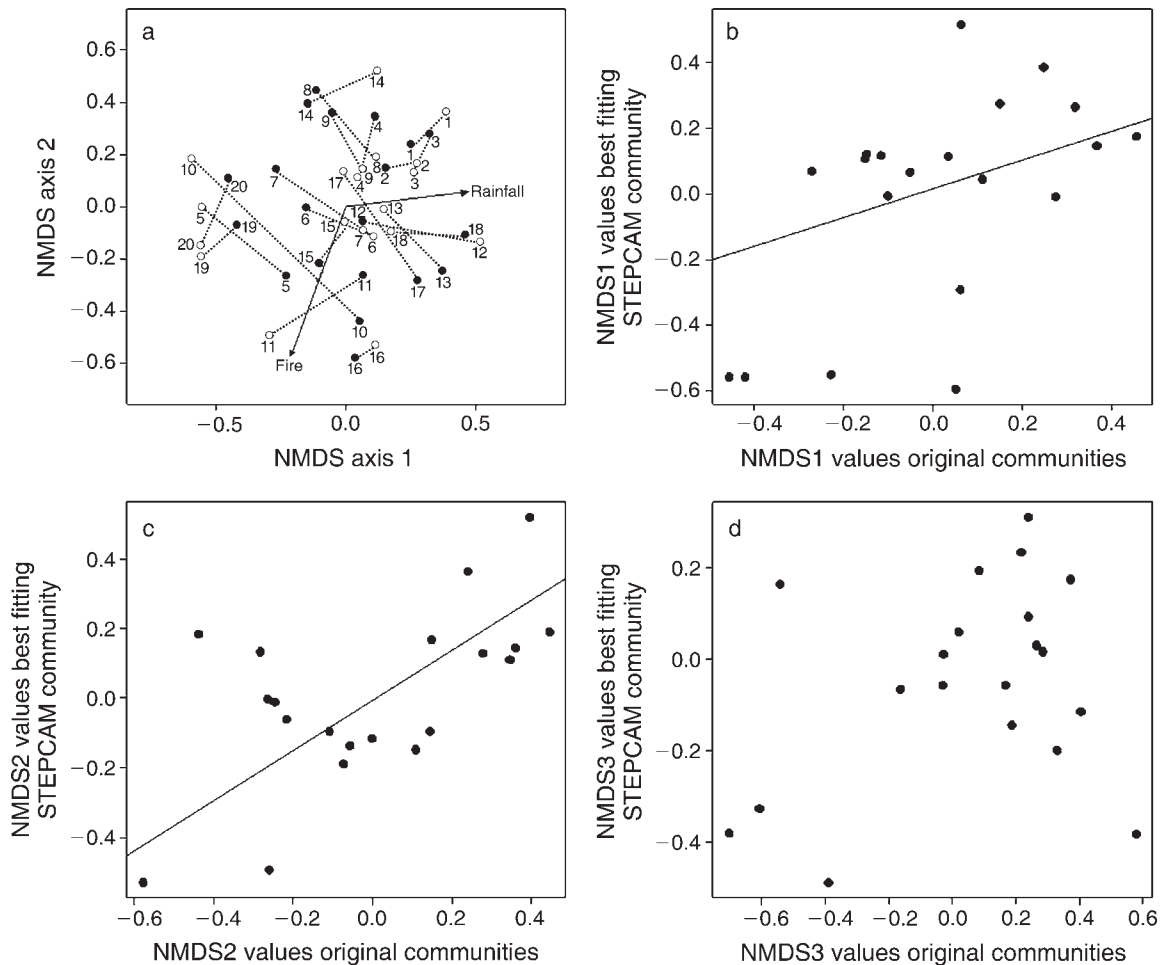


FIG. 5. Species compositions of both observed and simulated communities. (a) The first two nonmetric multidimensional scaling (NMDS) axes, with observed communities shown in dark gray and simulated communities shown in light gray. (b–d) NMDS values of simulated communities against NMDS values of observed communities, including significant ($\alpha = 0.05$) regression lines. Correlations between NMDS values of observed and simulated communities were $r^2 = 0.286$, $P = 0.00885$ (NMDS1); $r^2 = 0.338$, $P = 0.00427$ (NMDS2); $r^2 = 0.058$, $P = 0.157$ (NMDS3).

2012, Shipley et al. 2012, Martorell and Freckleton 2014), our STEPCAM approach has two main advantages. Firstly, while other approaches are biased toward the detection of filtering processes (Laughlin and Laughlin 2013), our approach explicitly incorporates limiting similarity processes, and as demonstrated, it is able to distinguish between these processes. Another merit of our new approach is that it builds upon the already existing and popular approach of null model comparisons of trait distributions. In fact, null models, which simulate community assembly by randomly drawing species from a species pool, reflect a specific parameter setting (100% dispersal assembly) of our more general STEPCAM approach. This makes outcomes of our STEPCAM approach easy to compare with traditional approaches, while also allowing more specific insights into community assembly by estimating the relative contribution, rather than just the presence, of different community assembly processes.

Nevertheless, we recognize that future modifications could substantially improve our approach. While ecological processes primarily act at the level of the individual, our models are species-based. In future implementations, STEPCAMs could become individual-based and take species abundances and intraspecific trait variation into account, thereby also allowing for intraspecific interactions. Future studies could also alter the weightings by which traits affect functional diversity metrics, thus recognizing that, depending on the context, some traits are functionally more important than others. We chose not to do this, since we had no strong a priori expectations of which traits are most important for community assembly of this savanna system. While we assumed that different processes act additively upon community assembly, in real life, different processes might interact (e.g., through priority effects), which merits further study. Also, using additional characteristics of communities or species pools (e.g., community

turnover; phylogenetic data), orthogonal or alternative to the metrics we already used, might lead to additional insights in community assembly. Although these demanding (in terms of both data and computational power) modifications were not feasible for this study, we highly welcome future studies incorporating these. Ultimately, however, approaches like these should be combined with experiments (as outlined in, e.g., Adler et al. [2013]) to verify conclusions based on observational data.

When we applied our method to fit trait distributions of 20 observed savanna tree communities, we found that the best-fitting models consisted mostly of dispersal assembly steps (on average 75.8%), less of filtering steps (18.8%), and least of limiting similarity steps (5.4%). Therefore, niche-based processes might be less important for the assembly of savanna tree communities than we anticipated. During a dispersal assembly step, the chance of a species being removed was inversely proportional to its frequency in the species pool. Hence, we assumed a lack of species differences in dispersal capability. Both the fact that the surveyed area of our study is relatively small (30×30 km) and the fact most species have similar seed dispersal strategies (Pooley 1997) may explain why our results were largely in line with this assumption. Many purely neutral models (e.g., Hubbell 2001) also assume that (1) niche-based processes are not important for community assembly and (2) the chance of successful dispersal of a species is proportional to its abundance in the metacommunity (thus assuming that all individuals are equally likely to successfully disperse). However, it should be emphasized that dispersal assembly was not the only process shaping communities; rather, we found statistical evidence that it was the dominant one when compared to the influence of (two types of) niche-based processes.

An interesting question is why in a system with some very clear constraints on tree recruitment and growth (e.g., due to drought, fires, and herbivory), community assembly nevertheless appears very stochastic, with on average 75.8% of the steps of best-fitting STEPCAMs being non-niche based. Part of the answer lies in our definition of the species pool, which only included species found in our set of 20 plots. Therefore, larger-scale filtering processes that determine which species can or cannot occupy any of our research area are ignored in this study, which might partially affect outcomes (Garzon-Lopez et al. 2014). Also, the inclusion of other important traits, such as seed size (related to reproductive strategy) or rooting depth (related to nutrient uptake) might have led to a higher detection of niche-based processes than the current set of traits. Nonetheless, within our study design, there are steep rainfall and fire gradients (see Appendix: Fig. A1A, B) and average trait values do respond to these (Appendix: Table A8.1). So the question remains why tree communities sampled over these gradients appeared relatively randomly (75.8% of the steps of best-

fitting STEPCAMs were non-niche based) assembled with respect to the traits we measured. One reason might be that species have different strategies to cope with the same kinds of conditions, as has been shown in studies related to herbivory (Bryant et al. 1989). This can result in contrasting phenotypes with similar fitness (Marks and Lechowicz 2006). In addition, it might be that intraspecific variation is large when compared to interspecific trait variation. Taken together, organisms of different species could be functionally equivalent (Hubbell 2001, 2006) despite differences in traits, leading to the emergence of neutral-like trait distributions.

Although less so than dispersal assembly processes, filtering and limiting similarity still explained part of the observed trait distribution patterns of tree communities. Filtering was especially important in areas with high fire frequency. Fire is a commonly recognized stress factor for savanna trees (e.g., Bond and Wilgen 1996) and may thus have been responsible for the imprints of filtering on trait distribution patterns. Additionally, filtering patterns might have been caused by the exclusion of competitively inferior tree species (Mayfield and Levine 2010). Limiting similarity is usually interpreted as an indicator of interspecific competition (Hutchinson 1959, MacArthur and Levins 1967, Abrams 1983, Cornwell and Ackerly 2009). In savannas, where tree growth is limited by water availability, fires, or grasses (e.g., Bond and Wilgen 1996, Scholes et al. 2002, Cramer et al. 2010) and canopies are quite open, light competition among trees is in most cases likely to be modest (van der Plas et al. 2013). Sites with low fire frequency and high rainfall (a rare combination, as rainfall promotes fuel load) may be among the few locations where light competition among trees is strong enough to detect high impacts of limiting similarity. Interestingly, these were also the sites with the highest species richness (Appendix: Table A8), suggesting a possible relationship between species richness and the presence of limiting similarity processes, which merits further study.

When comparing the outcomes of our STEPCAM approach with traditional null model outcomes, one main observation is that while classic null models never detected any sign of limiting similarity in our data set, our novel STEPCAM approach did. Limiting similarity and filtering are expected to have more or less opposite effects on the trait distributions of co-occurring species (Weiher et al. 2011). Therefore, the impact of one of these processes can potentially mask the effect of the other. Although other studies have suggested solutions for these problems (e.g., Helmus et al. 2007, Cornwell and Ackerly 2009, Parmentier et al. 2014), these solutions are unlikely to work under all circumstances and do not quantify the relative importance of co-occurring processes. We have shown that the traditional assumption that filtering decreases trait diversity, while limiting similarity increases it, is a highly simplified one, as the combination of these processes

causes nonlinear patterns in parameter space (Fig. 2). Therefore, when limiting similarity processes and filtering processes operate simultaneously, at similar spatial scales, it may be very hard to statistically detect both these processes using null models and even impossible to quantify the relative contributions of these different processes to community assembly. With our STEPCAM approach, we made progress in overcoming these problems, which explains why we could detect imprints of limiting similarity. We therefore suggest that our approach is promising to unravel the relative importance of different community assembly processes across different types of ecosystems, types of communities, trophic levels, and global environmental gradients.

ACKNOWLEDGMENTS

We thank Nelly Eck for helping with the chemical analyses and Francisco Encinas Viso and Adriana Alzate Vallejo for useful discussions. A. Ordóñez is supported by the HISTFUNC project (ERC Starting Grant 310886) and H. Olff and R. S. Etienne are funded by the NWO. We would also like to thank the Center for Information Technology of the University of Groningen for their support and providing access to the Millipede high performance computing cluster. We also thank Jesse Lasky and two anonymous reviewers for providing useful suggestions on earlier versions of this article.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix and Supplement are available online: <http://dx.doi.org/10.1890/14-0454.1.sm>